THE ANNALS

AND

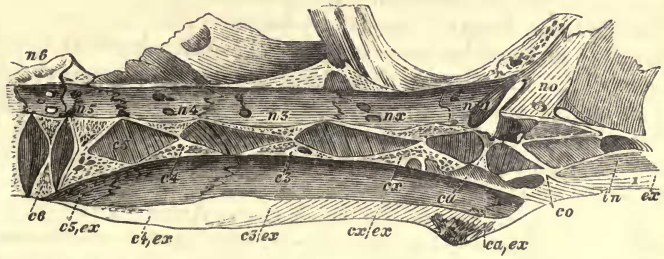
MAGAZINE OF NATURAL HISTORY.

No. 133. OCTOBER 1847.

XX.—*Description of the Atlas, Axis, and Subvertebral Wedge Bones in the* Plesiosaurus, *with remarks on the homologies of those bones.* By Prof. Owen, F.R.S.

In my 'Report on British Fossil Reptiles*' two explanations are offered of the special homologies of the subvertebral wedge-bones discovered by Sir P. de M. Grey Egerton in the neck of different species of *Ichthyosaurus*†,—the one as repetitions of the 'odontoid process,' the other as of the so-called 'body of the atlas' in existing reptiles. Viewing the subvertebral wedge-bones in their wider relations, I subsequently described them as "detached developments of bone in the lower part of the capsule of the notochord" (*chorda dorsalis*, auct.); illustrating that view by reference to the condition of the corresponding part of the vertebral column in a large Siluroid fish‡. Subjoined is a figure of that remarkable structure (fig. 1); in which *c o* is the basi-

Fig. 1.



Section of anchylosed cervical or anterior abdominal vertebræ of *Bagrus tachypomus*, nat. size.

* Report of British Association, 8vo, 1839, pp. 100, 101.
† Geological Transactions, 2nd ser. vol. v. p. 187. pl. 14, 1836.
‡ Report on Vertebrate Skeleton, Rep. Brit. Assoc. 1846, p. 260.

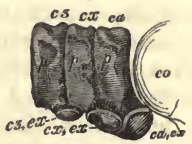
occipital or centrum of the occipital vertebra; *i n* its internal or medullary structure; *e x* its cortical compact portion: the arrest of ossification in the posterior part of its medullary portion has left the deep concavity turned towards the atlas, and which was filled by the liquified remains of the gelatinous part of the notochord; but continuous ossification in the notochordal capsule has anchylosed the cortical part of the occipital centrum (*e x*) with that (*c a, e x*) of the centrum of the atlas. *c a* is the ossified medullary part of the centrum of the atlas; *n o* is the neural arch of the occipital vertebra; *n a* the neural arch of the atlas, separated from its centrum; *c x*, central part of the body of the axis; *c x, e x*, cortical part of ditto; *n x*, neural arch of the axis perforated by the motory and sensory roots of the nerves separately; *c* 3, central part of body of third vertebra; *c* 3, *e x*, cortical part of ditto; *n* 3, neural arch; *c* 4, central part of body of fourth vertebra; *c* 4, *e x*, cortical part of ditto; *n* 4, neural arch of ditto; *c* 5, central part of body of fifth vertebra; *c* 5, *e x*, cortical part of ditto; *n* 5, neural arch of ditto. Here the vertebræ begin to exchange their elongated figure for the ordinary short one, which is exemplified in *c* 6, where they begin to be free.

In the fish-like batrachians, the Menopome for example, the body and neural arch of the atlas have coalesced: the anterior zygapophyses descend from the fore-part of the neural arch upon the sides of the fore-part of the centrum which projects forwards between them, like an odontoid process: the articular surfaces of the zygapophyses (oblique or articular processes of human anatomy) are subcircular, slightly concave, directed forwards and a little upwards: they receive the convex zygapophyses or condyles of the coalesced exoccipitals. The posterior zygapophyses of the atlas have also large subcircular articulations directed downwards. The body of the atlas appears to have been developed at the expense of the central part of the notochord, which forms the anterior convex part which articulates with the basi-occipital plate at the bottom of the foramen magnum. A deep concavity at the back part of the atlas contains the unossified remnant of the central or gelatinous part of the notochord.

In the extent, however, to which the centrum of the atlas is ossified, the Menopome and other perennibranchians resemble the fishes. If, indeed, the persistent portion of the notochord which fills the anterior concavity of the atlas and the posterior concavity of the basi-occipital in the Siluroid or other osseous fish were ossified and anchylosed to the atlas, that vertebra would closely resemble the atlas of the Menopome, and I regard the singular modification of form which the atlas of the Menopome presents, as compared with that of the osseous fish, to be due to

the above-described ossification of the anterior end of the central part of the notochord. If, on the other hand, such ossified part of the notochord were to coalesce with the basi-occipital instead of with the atlas, it would form a tubercle on the back part of the occipital centrum which would fit into the concavity left on the fore-part of the centrum of the atlas. Now this is precisely what has happened in those large extinct fish-like reptiles, the Enaliosauria (fig. 2). That is to say, the basi-occipital presents a convex condyle (*c o*) which is received into a cavity on the fore-part of the body of the atlas *c a*, completed below by the first 'wedge-bone' *c a*, *e x*. The main or central part of the body of the atlas, *c a*, as Sir P. Egerton has shown, is early anchylosed to the body of the axis, *c x*; and, in a specimen in which he succeeded in separating the two vertebræ, they were applied to one another by flat and even surfaces. Into the lower part of this speedily obliterated symphysis a second distinct ossicle (*c x, e x*) is wedged, a similar but smaller ossicle (*c* 3, *e x*) being situated at the inferior interspace between the axis and third vertebra.

Fig. 2.

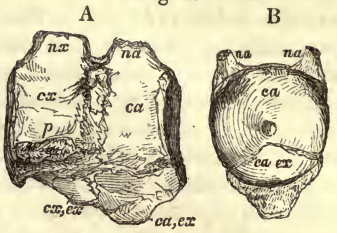


Anterior cervical vertebræ, *Ichthyosaurus*.

The condition of the anterior vertebræ of the large Siluroid fish (fig. 1), in which I found the central biconcave parts of the bodies of the atlas, axis, and three succeeding vertebræ established by distinct ossification of the central part of the notochord, whilst the whole were attached below to a continuous ossification in the capsule of the notochord, will explain what is meant by the statement that the subvertebral wedge-bones of the *Ichthyosaurus* are derived from "detached developments of bone in the lower part of the capsule of the notochord," at the inferior interspace between the occiput and atlas, and at the similar interspaces of the two or three succeeding cervical vertebræ; but varying in number in different species.

A recent opportunity of examining the atlas and axis of the *Plesiosaurus*, kindly afforded me by my friend Prof. Sedgwick, has not only strengthened this view of the general nature of the 'subvertebral wedge-bones,' but has made me incline to the second hypothesis of the special homology of the first or anterior of the wedge-bones, which is proposed in my 'Report on British Fossil Reptiles,' viz. that it answered to the part described as the body of the atlas in the existing Saurians and Chelonians; which therefore may be regarded, like the first subvertebral wedge-bone, as the cortical part only of such vertebral body, like the plate of bone beneath the biconcave central part of the body of the atlas in the Siluroid fish.

Fig. 3.



Anchylosed atlas and axis, *Plesiosaurus pachyomus*, reduced.

The atlas and axis in the *Plesiosaurus* (fig. 3) preserve the general proportions of the other cervical vertebræ, and are consequently longer than their homologues in the *Ichthyosaurus*; but they are similarly anchylosed together, and measure $4\frac{1}{2}$ centimeters (nearly 2 inches) in length, 3 centimeters across the anterior concave surface of the atlas, and $3\frac{1}{2}$ centimeters across the less concave posterior surface of the axis: the neural arch of each vertebra has coalesced with its centrum; and a long obtuse process is formed below by a similar coalescence of the first and second 'wedge-bones' with each other and with their respective centrums. The limits of the anterior 'wedge-bone,' *c a, e x*, are traceable: it is proportionally larger than in the *Ichthyosaurus* (fig. 2), in which it is likewise larger than the succeeding wedge-bones. It forms in the *Plesiosaurus* the lower third part of the atlantal cup for the occipital condyle B, *c a, e x*; the anchylosed bases of the neurapophyses (*n a*) form the upper border of the cup, and the intermediate part or bottom of the cavity is formed by the centrum of the atlas (*c a*), or rather by that part which, like the biconcave centrum in the Siluroid fish, is developed from the central portion of the notochord.

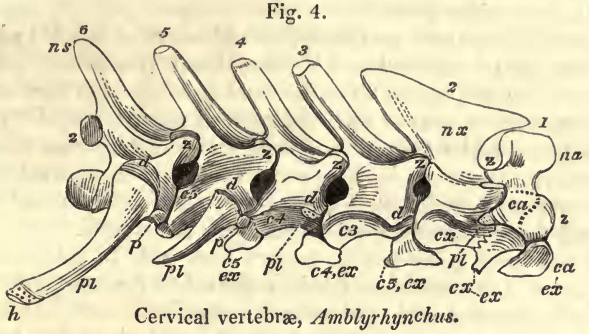
The smaller or second wedge-bone (*c x, e x*) is lodged in the inferior interspace between the atlas and axis, but has coalesced with both bones, as well as with the large anterior wedge-bone or cortical part of the body of the atlas, *c a, e x*. This anterior wedge-bone developes a thick but short rough tuberosity from its under part, but there is no distinct second tuberosity from the second wedge-bone: both, indeed, have so coalesced together as to parallel the continuous ossification of the under part of the notochordal capsule beneath the central parts of the bodies of the atlas and axis in the Siluroid fish (fig. 1, *c a e x, c x e x*, &c.). There is no transverse process from the centrum of the atlas of the *Plesiosaurus*; but the fractured base of a depressed parapophysis, *p* (lower transverse process), or anchylosed rib, projects from each side of the proper centrum of the axis.

In a large Iguanoid lizard (*Amblyrhynchus*) the part answering to that described by Cuvier as the body of the atlas in the Monitor and Crocodile* has the form of a wedge (fig. 4, *ca, e x*)

* Ossem. Foss. v. pt. 2. p. 96.

like the first wedge-bone in the *Plesiosaurus*, and forms the lower third part of the cup for the occipital condyle: it articulates be-

Fig. 4.



Cervical vertebræ, *Amblyrhynchus*.

hind to a second similarly-shaped wedge-bone (*cx*, *ex*); above to the part *c a*, (indicated by the dotted outline on the neural arch of the atlas which covers it,) which answers to the body of the atlas, or rather the central part of the body of the atlas, in the *Plesiosaurus* (*c a*, fig. 3); but which there also immediately supports the neural arch (*n a*), whilst in the recent Saurian the base of each neurapophysis (*n a*, fig. 4) descends to rest upon the angles of the base of the 'wedge-bone' (*c a*, *e x*) which represents the inferior peripheral part of the body of the atlas. The interspace between the bases of the neurapophyses is occupied by the distinct ossicle (*c a*) which adheres closely by a flat surface to the body of the axis (*c x*), and forms the bottom of the articular concavity for the occipital condyle: it is the part described by Cuvier as 'pièce analogue à l'odontoïde' in the Monitor*, and it is plainly the homologue of the part of the body of the atlas which is joined by a flat surface, and early anchylosed, to the body of the axis in the *Plesiosaurus* and *Ichthyosaurus*. In the existing Lacertians the 'odontoïde' differs, however, from the anchylosed atlas of the Enaliosauria by taking no share in the support of the neurapophyses of the atlas: the ossification of these has obviously extended deeper into the sides of the notochordal capsule, so that they articulate directly with the wedge-bone (*c a*, *e x*) developed in the inferior part of that capsule: and the central ossification (*c a*) adapted to the lower half of such atlantal vertebral ring is proportionally reduced. The first 'wedge-bone' or cortical part of the body of the atlas (fig. 4, *c a*, *e x*) is carinate below in the *Amblyrhynchus*, and the keel is produced backwards into a short spine. The second 'wedge-bone,' *c x*, *e x*, is similarly shaped, but rather larger than the first. Its base articulates behind with the body of the axis, *c x*, above with the odontoid piece, *c a*, and

* Ossem. Foss. v. pt. 2. p. 283.

in front with the wedge-shaped cortical part of the body of the atlas *c a*, *e x*. The lower part of the second wedge-bone is produced into a short spine.

There is a distinct cartilaginous rudiment of a rib (*pleurapophysis, pl,* 1) attached to the diapophysis (transverse process from the neural arch) of the atlas, and another from that of the fourth vertebra (*pl,* 4). The first ossified pleurapophysis (*pl,* 5) occurs on the fifth vertebra; and beneath the diapophysis supporting this rib, there is a cartilaginous rudiment of a parapophysis (*p*); the same is still more plainly seen in the sixth cervical vertebra, but the heads of the pleurapophyses are simple.

The odontoid piece (*c a*) is convex from side to side, concave from above downwards; is firmly attached to the fore-part of the body of the axis and to the second wedge-bone, but with visible traces of the suture remaining. The lower part of the body of the axis is carinate, but not produced into a spine. A third separate ossification in the capsule of the notochord (*c* 3, *e x*) is wedged into the inferior interspace between the axis and third vertebra; and similar but successively smaller wedge-bones (*c* 4 *e x*, *c* 5 *e x*) are articulated between the fourth and fifth, fifth and sixth, and also between the sixth and seventh vertebræ in the *Amblyrhynchus*. If the odontoid process be interpreted as the homologue of the anterior anchylosed body of the atlas in the *Plesiosaurus*, the first wedge-bone will stand in the same relation to it as the second wedge-bone does to the axis, the third to the third vertebra, the fourth to the fourth, and so on. These wedge-bones are plainly the special homologues of the 'subvertebral wedge-bones' discovered by Sir P. Egerton in the *Ichthyosaurus*; but their general homology is open to two interpretations. They are, no doubt, autogenous ossifications in the under part of the capsule of the notochord; but, as such, may be interpreted either as parts of the cortical layer of the centrum of their respective vertebræ, or as rudimentary hæmapophyses and imperforate homotypes in the neck of the hæmal arches and spines in the tail*. According to the latter view, what has usually been regarded as the centrum or body of the atlas in Saurians, Chelonians, and the higher Vertebrata would be the hæmapophysis of that vertebra; and the odontoid process the true centrum. But against this view militates the constant relation of the inferior wedge-shaped bone of the atlas in Saurians, Chelonians and higher Vertebrates to the neurapophyses, as immediately supporting them and completing with them the neural arch. The obvious serial homology, also, of that lower part of the atlas (*c a*, *e x*) with the basi-occipital and basi-sphenoid leads me to conclude that, like them, it is the

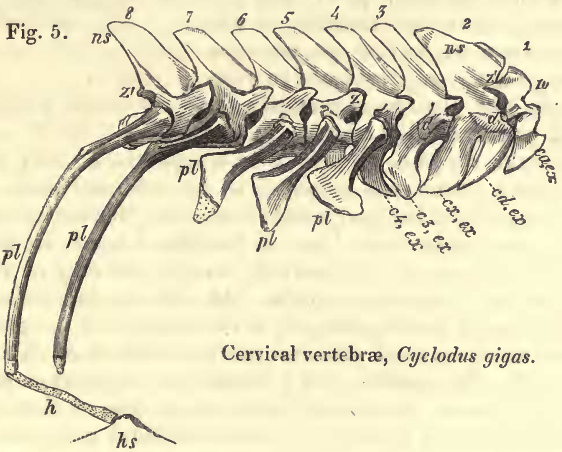
* In the *Bagrus*, in fact, the corresponding ossification of the notochordal capsule is actually perforated by the aorta.

inferior cortical part of the body of its vertebra. In the cranial vertebræ this usually depressed and expanded cortical part, exemplified by the basi-occipital, basi-sphenoid, presphenoid and vomer, is the sole representative of the centrum of such vertebræ: in the atlas the odontoid process would represent the central part also of the body of the vertebra, but detached from the cortical part.

The following facts, however, appear to oppose themselves to the determination of the 'odontoid' as the central part of the body of the atlas.

In the great Australian Skink (*Cyclodus gigas*) the second wedge-bone (fig. 5, *o d, e x*), which is developed into a long spine

Fig. 5.



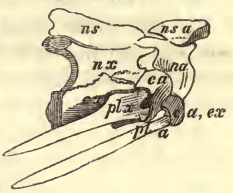
Cervical vertebræ, *Cyclodus gigas*.

and is anchylosed to the under part of the odontoid piece, is not the only inferior or hæmal spine of the axis vertebra; but a second broader and longer spine (*c x, e x*) is developed from the under part of the proper body of the axis. And the fact of the absence of any suture between this spine and the body of the axis is not enough to support the conclusion that it is a mere excess of development of the under part of the body of the axis and no true homotype of the inferior spines or wedge-bones; because, besides the anchylosis of the preceding spine (*o d, e x*) with the odontoid piece, the fourth spine (*c* 3, *e x*) is equally anchylosed with or developed from the whole under part of the third cervical vertebra of the *Cyclodus*; and the fifth spine (*c* 4, *e x*) is a similarly continuous process from the under part of the fourth vertebra. As the odontoid piece and its spine are completely anchylosed with the axis, this vertebra presents the anomalous structure of one neural spine and two consecutive hæmal spines. The above-described structure of the anterior vertebræ of the

neck of the *Cyclodus gigas* gives some colour to the view of the odontoid as the rudiment of a vertebra distinct from both atlas and axis, and which in the *Cyclodus* is represented by the centrum and hæmal spine, without the neural arch.

The structure of the atlas and axis in the Crocodile (fig. 6) gives further colour to this view. The odontoid piece (*c a*) is wholly interposed between the wedge-shaped cortical part of the body of the atlas, *c a, e x,* and the body of the axis, *c x*: moreover the wedge-bone, *c a, e x,* not only supports neurapophyses, *n a,* but also pleurapophyses, *pl a*: and the odontoid, *c a,* in like manner, besides giving some support to the neurapophyses, *n x,* also supports, and that exclusively, the pleurapophyses, *pl x,* or second pair of cervical ribs.

Fig. 6.



Atlas and axis of the Gavial.

The true centrum of the axis *c x* supports no ribs, and appears like an enormous epiphysis to *c a,* extended backwards to aid in supporting the long neural arch *n x*. Neither the odontoid *c a,* nor the wedge-shaped part of the atlas *c a, e x,* are produced into inferior spines. If however, as the anatomy of the atlas and axis in Lacertian Saurians has led me to conclude, the odontoid *c a* is the homologue of the anterior (*c a,* figs. 2 & 3) of the two anchylosed vertebral centrums described as atlas and axis in the Enaliosaurs, the bifurcate pleurapophysis *pl* in the Crocodile should be the displaced homologue of that which is articulated to the posterior of those vertebral centrums in the *Ichthyosaurus,* and the articular surface of which is shown at *p, c x,* A, fig. 3, in the *Plesiosaurus,* and by Sir P. Egerton in pl. 14. fig. 2. B *d* of his Memoir above-cited, in the *Ichthyosaurus*. Whether the anterior vertebra *c a,* fig. 2, may also have supported by the surface *p,* a rib, homologous with that of the atlas of the Crocodile *pl a,* is uncertain; but, if so, the atlantal rib in the Crocodile would show, in like manner, a displacement forwards, from the central part of the body *c a,* represented by the odontoid piece in recent Saurians, to the first subvertebral wedge-bone *c a, e x,* which represents the body of the atlas in such Saurians, and takes a share in the support of the neural arch, which its homologue does not do in the *Ichthyosaurus* and *Plesiosaurus*. If, however, the hypothesis that *c a,* fig. 6, in the Crocodile is the homologue of the anchylosed atlas *c a,* figs. 2 & 3, of the Enaliosaurs, and that *c a, e x,* fig. 6, is the homologue of the first wedge-bone, *c a, e x,* fig. 2, be saved by assuming an advanced displacement of the pleurapophyses *pl x* and *pl a,* in the Crocodile, the numbers and relations of the inferior spines in the great

Cyclodus do not lend themselves so readily to the same determination of the odontoid in that lizard, as a part or complement of the body of the first vertebra.

The number of the inferior spines might be made to correspond with that of the vertebræ by supposing either *o d*, *e x*, or *c x*, *e x*, in fig. 5, to be an accessory exogenous process, and not a true homotype of the other four spines; or the spine *c x*, *e x*, may be held to belong properly to the third vertebra, and with the succeeding spines to be abnormally advanced and anchylosed to the vertebra anterior to the one to which it properly belongs. Yet both these suppositions appear to be equally arbitrary. The condition of the odontoid and axis in the *Cyclodus* is, nevertheless, an exceptional one in the Lacertia, and I no longer regard the distinct inferior spine *c x*, *e x*, in fig. 5, as a proof that the odontoid, like the atlas, is the homologue of one of the subvertebral wedge-bones. I still retain the opinion that it is not "the peculiarly developed anterior articular epiphysis of the second vertebra"*; but I return to my former idea of the special homology of the odontoid piece in Saurians, and consequently the odontoid process in mammals, with the part called the anchylosed atlas in the *Ichthyosaurus*; and the subsequently ascertained structure of the parts in the *Plesiosaurus* has confirmed the conclusion that the first subvertebral wedge-bone in the *Ichthyosaurus* and *Plesiosaurus* represents the part which has been called 'body of the atlas' in existing reptiles, but is reduced to a still more atrophied condition than in them†.

With respect to the general homology of these parts, the first wedge-bone is a detached part of the cortex of the body of the atlas, and the so-called atlas in the *Enaliosauria* or the odontoid piece in existing *Sauria* is the central ossification of the same vertebral element. The anchylosis of the atlas and axis is no longer, therefore, a peculiarity of the Enaliosauria, but a structure essentially repeated in every higher vertebrate form up to Man, in whom the anchylosed part of the atlas bears the anthropotomical name of 'odontoid process.' It might be expected that the segment immediately succeeding those of the skull would be the seat of more extensive and remarkable modifications than the succeeding vertebræ of the trunk, and each modification will be found, as the habits and mode of life of the different species become better known, to be expressly adapted to such habits. But such recognition of final causes by no means precludes the necessity for every legitimate attempt to uplift the veil which hides the type upon which all the adaptive modifications of the endoskeleton are based.

* Report on Archetype of Vertebral Skeleton, 1846, p. 261.

† Report on British Fossil Reptiles, 1839, p. 101.